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Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution

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Abstract: The globally increasing light pollution is a well-recognized threat to ecosystems, with negative effects on human, animal and plant wellbeing. The most well-known and widely documented consequence of light pollution is the generally fatal attraction of nocturnal insects to artificial light sources. However, the evolutionary consequences are unknown. Here we report that moth populations from urban areas with high, globally relevant levels of light pollution over several decades show a significantly reduced flight-to-light behaviour compared with populations of the same species from pristine dark-sky habitats. Using a common garden setting, we reared moths from 10 different populations from early-instar larvae and experimentally compared their flight-to-light behaviour under standardized conditions. Moths from urban populations had a significant reduction in the flight-to-light behaviour compared with pristine populations. The reduced attraction to light sources of 'city moths' may directly increase these individuals' survival and reproduction. We anticipate that it comes with a reduced mobility, which negatively affects foraging as well as colonization ability. As nocturnal insects are of eminent significance as pollinators and the primary food source of many vertebrates, an evolutionary change of the flight-to-light behaviour thereby potentially cascades across species interaction networks.

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1 **Reduced flight-to-light behaviour of moth populations**
2 **exposed to long-term urban light pollution**

3
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18

Abstract

The globally increasing light pollution is a well-recognised threat to ecosystems, with negative effects on human, animal and plant wellbeing. The most well-known and widely documented consequence of light pollution is the generally fatal attraction of nocturnal insects to artificial light sources. However, the evolutionary consequences are unknown. Here we report that moth populations from urban areas with high, globally relevant levels of light pollution over several decades show a significantly reduced flight-to-light behaviour compared to populations of the same species from pristine dark sky habitats. Using a common garden setting, we reared moths from ten different populations from early instar larvae and experimentally compared their flight-to-light behaviour under standardised conditions. Moths from urban populations had a significant reduction in the flight-to-light behaviour compared to pristine populations. The reduced attraction to light sources of “city moths” may directly increase these individuals’ survival and reproduction. We anticipate that it comes with a reduced mobility, which negatively affects foraging as well as colonization ability. As nocturnal insects are of eminent significance as pollinators and the primary food source of many vertebrates, an evolutionary change of the flight-to-light behaviour thereby potentially cascades across species interaction networks.

39 **Background**

40 Anthropogenic light pollution is recognized as a global environmental change
 41 negatively affecting humans [1], animals [2, 3], and microbes [4]. The negative
 42 effects are well known and even captured in the Shakespearian saying “Thus hath the
 43 candle singed the moth”, referring to someone tempted by something that eventually
 44 will lead to its downfall. As a global phenomenon [5, 6], light pollution is a by-
 45 product of urbanization [6] and interferes with the natural day-night cycle, resulting in
 46 changed phenologies of organisms in the polluted habitat [7]. An even more direct
 47 effect of light pollution is the widely observed attraction of organisms ranging from
 48 migrating birds to insects to the light sources, which can result in increased mortality
 49 through direct burning or increased exposure to predators [e.g., 8, 9]. Furthermore,
 50 attraction to light may lure organisms out of their native habitat and interfere with
 51 normal feeding behaviour, mating, and reproduction [3]. The negative effects of light
 52 pollution on community composition [4, 10], population dynamics and organisms’
 53 Darwinian fitness [11] have been globally documented, and mortality at artificial light
 54 sources can be 40- to 100-fold higher than in dark-sky populations [e.g., 3, 8].

55 Surprisingly, however, little is known about the potential evolutionary
 56 consequences. Existing data show that there is a high variability among species and
 57 sexes to be attracted by light [12, 13], and anecdotal evidence from naturalists even
 58 indicates within-species variation [14]. Given the detrimental effect of the flight-to-
 59 light behaviour in polluted areas it has been postulated that natural selection should
 60 favour individuals with a lower propensity of being attracted by light [7, 12].

61 Organisms’ phenotypic and genetic responses to anthropogenic environmental
 62 changes are well-known, such as the classic example of industrial melanism of the
 63 peppered moth. However, possible selective responses to light pollution have not yet

been documented, even though artificial night lighting has strongly increased over the last decades [3], has a pronounced geographic variation [6], and is having increasingly negative effects on many species [3], creating the necessary conditions for directional selection and adaptation to a novel anthropogenic stressor. Here, we report an experimental quantification of a reduced flight-to-light behaviour of small ermine moths from populations occurring in areas with high light pollution compared to populations with low pollution.

Methods

Study organism and study sites

We used the small ermine moth (*Yponomeuta cagnagella*), which is widely distributed across Europe. Its larvae strictly feed on European spindle (*Euonymus europaeus*) [15]. Larvae live in loose silk-webs, forming gregarious full-sib groups on their host plants. In order to test for an effect of multi-generational exposure to artificial light pollution on flight-to-light behaviour, we collected larvae of the small ermine moths in areas with low to medium levels of light pollution ($<3 \cdot 10^{-9} \text{ W sr}^{-1} \text{ cm}^{-2}$; subsequently called dark-sky populations; table 1) and in areas which have been exposed to strong light pollution for several decades (current light pollution 20 to $>40 \cdot 10^{-9} \text{ W sr}^{-1} \text{ cm}^{-2}$; subsequently called light-polluted populations, data from <http://www.lightpollutionmap.info>) [6]. The latter populations were always sampled in the immediate vicinity of streetlights in urban parks or along streets (max. distance to light source 20–50 m).

Laboratory conditions

We collected second-instar larvae, such that organisms were independently sampled with respect to the subsequent experimental test method, in ten independent populations from locations in North-western Switzerland and in Eastern France in spring 2007 (table 1). These populations were not connected by suitable habitat and represented independent units. At each location, larvae from multiple full-sib family clutches were collected. Some of these populations had been used in a previous analysis on sex-specific flight-to-light behavior [12]. Larvae were reared in the laboratory under standardized, common garden conditions in 500-ml plastic boxes at 80% relative humidity and a daily light-dark cycle of L16:D8 h, including 1 h dusk and dawn phases. Temperature was 23 °C during the light phase, and 19 °C during the dark phase. Food was provided *ad libitum*.

Flight-to-light experiment

We experimentally tested the flight-to-light behaviour of small ermine moths in an indoor flight cage, measuring 5.7x2.5 m at the bottom, 5.7x1.8 m at the top, and of 3 m height (see Fig. S1 supplementary material). In this cage, moths can be attracted from every position, as the effective range of the light traps used is about 3–5 m [13]. Temperature and humidity in the flight cage was held constant at 20–22 °C and 60–80% relative humidity, respectively.

A standard Heath trap equipped with a fluorescent tube (Philips, Eindhoven, TL 6W/05; see Fig. S2 supplementary material) was placed at the long-end side of the flight cage. Previous to the experiment, adult moths were individually marked and kept at L16:D8 cycle such that they adapted physiologically to the day-to-night change. For the flight-to-light experiment, we used individuals two to three days post eclosion before they were sexually mature. We thereby pooled individuals from

different families and populations of origin. Moths were released at the opposite end of the lamp, and the tests started at the onset of dusk. The species flies generally at night and is not only crepuscular. We recorded the number and identity of all moths captured by the light trap versus all moths not attracted after 8 h.

Analysis

We used a generalized linear mixed effect model to test for a difference in flight-to-light behaviour of moths originating from light polluted areas versus dark-sky areas. As response variable we used the odds ratio of individuals attracted versus individuals not attracted, and a model with a binomial error distribution. Light pollution, sex and their interaction were included as fixed effects in the model, while populations and family nested within populations were included as random effects. Analyses were done in R version 3.0.1 [16].

Results

We tested the flight-to-light behaviour of 1048 adult moths (table 1). Individuals from the populations experiencing high light pollution had a significantly lower propensity to fly to light (Z -value= -2.1 , $p=0.036$; Fig. 1) than individuals from the populations from dark sky areas. Overall, the mean reduction in flight-to-light behaviour was 30% (36% reduction for males and 28% reduction for females). Furthermore, females were overall significantly less attracted by light ($[Z$ -value = 4.3 , $p < 0.001$, see also 12]). There was no significant interaction between population of origin and sex on the flight-to-light behaviour, and the interaction term was removed from the model. The sex ratio within populations did not deviate from 1:1 (mean \pm SE of females relative to males was 1.04 ± 0.11 , $p>0.8$).

Discussion

We experimentally showed that small ermine moths from populations exposed for many generations to high levels of light pollution common to urban and suburban areas have a significantly reduced propensity to fly to light compared to moths from dark sky populations. As moths and other insects attracted to artificial light are experiencing high levels of mortality and reduced fitness [e.g., 2, 8, 9], we interpret this as evidence for an adaptive response following Darwinian fitness selection caused by human induced change in environmental conditions. We cannot completely exclude that some of the observed effect was due to developmental differences based on the site of origin affecting adult behaviour or other selective agents associated with urbanization. However, as we collected the larvae at a very early stage (2nd instar) and raised them in a common garden, we think this is less likely than a common selective difference with respect to light pollution linked to urbanization.

The implications of our finding are important and manifold. First, a reduced flight-to-light behaviour may release natural populations from some of the negative consequences of artificial light pollution [2]. Specifically, there may be less direct mortality [8, 14] and lower predation risk [9, 10]. Second, the lower propensity for flight-to-light in city populations suggests that the original function of this behavior is in fact not essential for survival in urban landscapes. This might be because the adaptive value of this behaviour is generally weaker than the benefits of reducing this behaviour in light polluted environments. Alternatively, in illuminated urban environments the need to exhibit flight-to-light behaviour might be reduced. Third, a difference in the flight-to-light propensity between rural and urban populations may

bias biodiversity surveys based on commonly used light traps [13], in particular if populations of different species respond differently to changes in light condition.

Consistent with many other species, males are the more mobile sex in small ermine moths, and are thus also more often attracted to light [12]. Noteworthy, males from light-polluted habitats exhibited an almost identical flight-to-light behaviour as females from dark sky habitats (Fig. 1a). The reduced flight-to-light propensity, however, may come with a cost. Explanations for the reduced flight behaviour of moths originating from light-polluted populations include that these moths have a behaviourally or physiologically reduced perception or reaction to the light [14]. For example, size of the eyes, light-receptors in the eyes or information processing of perceived light might be altered. Alternatively, the reduced flight-to-light response may be caused by a decrease in overall mobility. Such a change could have far-reaching consequences, as a reduced mobility is known to negatively interact with habitat fragmentation and dispersal, to reduce flower visiting rates and pollination or take the moths out of the sky, and thus reduce prey availability for the nocturnal insectivores, such as bats or spiders.

Given the recent recognition of the light pollution effects acting on individuals to ecosystems, there have been calls to reduce light pollution and street light intensity [3]. While this is commendable, our demonstration of a presumably adaptive change in flight-to-light behaviour in populations having been exposed to long-term light pollution suggests that the effects of light pollution on natural populations may not necessarily vanish immediately when the lights were turned off, and that light pollution has already resulted in systematic changes in organisms' behaviour. This advocates for preventing light pollution, even at low levels, from spreading to areas

that are so far unaffected, in order to both reduce the direct negative effects of light pollution as well as to prevent long-term evolutionary changes.

Authors' Contributions

FA and DE developed the ideas, FA conducted the experiments, analysed the data and wrote a first draft of the manuscript. DE contributed substantially to interpretation and revisions of the manuscript. Both authors gave final approval for publication and agree to be held accountable for the content therein.

Data accessibility

Data available from the Dryad Digital Repository:
<http://dx.doi.org/10.5061/dryad.v1885> [17].

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Table 1. Localities of the 10 studied populations from France (F) or Switzerland (CH). Light pollution estimates are from taken from DataRadiance (see methods). These light-pollution values were measures in 2012, and we use them as a proxy for the last decade.

Site / country	Latitude/Longitude	Population	Light pollution (10^{-9} Watt /cm ² *sr)	# tested individuals
Blochmont / F	47° 26' 16" N 7° 14' 10" E	dark-sky	0.25–0.4	53
Kleinlützel / CH	47° 25' 55" N 7° 22' 57" E	dark-sky	0.4–1	93
Kiffis / F	47° 26' 18" N 7° 17' 59" E	dark-sky	0.4–1	89
Doucier / F	46° 39' 40" N 5° 41' 21" E	dark-sky	0.4–1	66
Lutterbach / F	47° 46' 12" N 7° 3' 36" E	dark-sky	1–3	19
Allschwil / CH	47° 32' 52" N 7° 32' 80" E	light-polluted	20–40	144
Reinach / CH	47° 31' 50" N 7° 36' 25" E	light-polluted	20–40	170
Hegenheim / F	47° 33' 43 "N 7° 31' 14 "E	light-polluted	>40	75
Basel Kannenfeld / CH	47° 33' 59" N 7° 34' 19" E	light-polluted	>40	129
Basel Spalentor / CH	47° 33' 28" N 7° 34' 53" E	light-polluted	>40	210

Legends

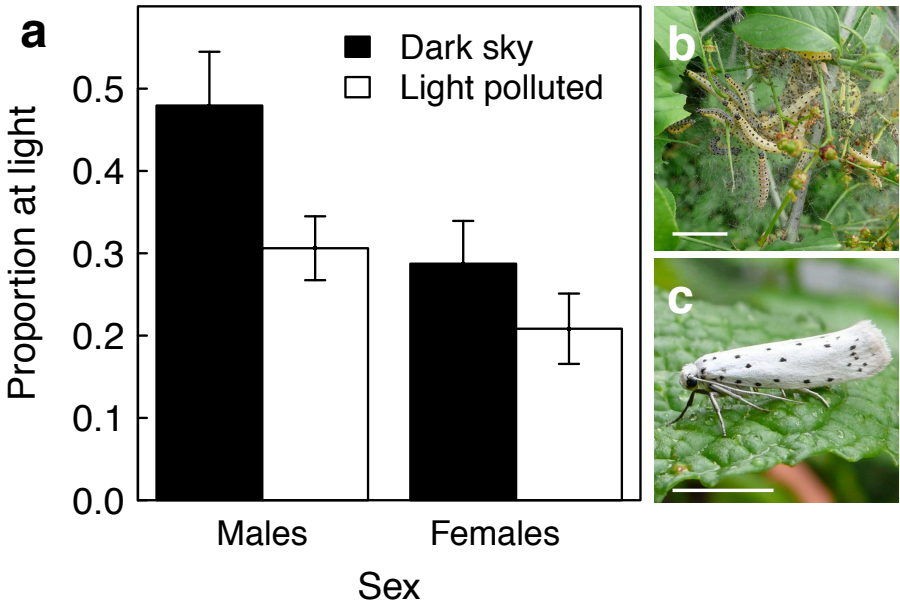


Figure 1. Flight-to-light behaviour of small ermine moths from dark sky and light polluted populations. a) Proportion (mean±SE across all populations) of small ermine moths attracted by artificial light under controlled experimental conditions. Overall, moths from populations which have been experiencing extensive light pollution are significantly less attracted to the light than moths from populations without light pollution (dark sky; $p=0.036$). b) Larvae of the small ermine moth (*Yponomeuta cagnagella*) on its host plant European spindle (*Euonymus europaeus*). c) Adult small ermine moth. Scale bar 5 mm.